MOLECULAR EVOLUTION IN AUSTRALIAN DRAGONS AND SKINKS: A PROGRESS REPORT

P.R. BAVERSTOCK AND S.C. DONNELLAN

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We have been using microcomplement fixation of albumin to assess the evolutionary relationships of the dragons and skinks of Australia, and to provide approximate dates of divergence of extant taxa. The results are preliminary, but suggest the following salient features. For the dragons: (1) The amphibolurid radiation is very recent, less than 20 MYBP; (2) *Moloch* is a part of the amphibolurid radiation; (3) the Australasian *Gonocephalus* are much more closely related to the amphibolurids and *Physignathus* than to Asian *Gonocephalus*; (4) the divergence of the amphibolurids, *Physignathus* and Australasian *Gonocephalus* occured in the mid-Miocene; (5) The Australasian agamids (including *Gonocephalus* and *Physignathus*) are closer to the African *Agama* than any Asian dragon so far tested. For the skinks: (1) The data are in accord with Greer's (1979) recognition of three groups of skinks in Australia, diverging about 60 MYBP; (2) The genus *Leiolopisma* is paraphyletic with the genera *Lampropholis, Carlia, Menetia* and *Morethia*; (3) The New Zealand *Leiolopisma* fall within the Australian *Leiolopisma* with a divergence time of about 20 MYBP. ☐ *Dragon, skink, microcomplement fixation, molecular clock, biogeography.*

P. R. Baverstock and S. C. Donnellan, Evolutionary Biology Unit, South Australian Museum, North Terrace, Adelaide, South Australia, 5000, Australia; P.R.B. present address: School of Resource Science and Management, University of New England, Northern Rivers, PO Box 159, Lismore, New South Wales, 2480, Australia; 17 August, 1988.

Five families of lizards occur in Australia - the Agamidae (dragons), Scincidae (skinks), Varanidae (goannas), Gekkonidae (geckos), and Pygopodidae (legless lizards). Of these, only the Pygopodidae are endemic to Australasia.

The last 15 years have seen enormous changes in our understanding of the generic and specific limits of Australian lizards, as a comparison of Worrell's (1963) book with Cogger's (1986) book reveals. Despite this work, the evolutionary origins and relationships among genera are often poorly known, and subject to very varied opinions (e.g. Tyler, 1979; Greer, 1979; Cogger and Heatwole, 1981; Witten, 1982). This uncertainty results from paucity of suitable morphological characters, high level of homoplasy in some groups, use of principally non-cladistic analyses, and paucity of fossils. It is in such areas that molecular genetic techniques can prove extremely valuable.

The molecular genetic approach to systematics and biogeography has two major contributions to make. Firstly, it provides a view of the evolutionary relationships of a group that is totally independent of that provided by morphology. This does not mean that it is the panacea for all problems in systematics. Rather, molecular genetic data should be seen as challenging established ideas about the evolution of a group, and highlighting areas of discrepancy. Secondly, there is mounting evidence that molecular genetic techniques can be used to provide a time-frame, albeit approximate, for the cladistic events in the evolution of a group (Wilson et al., 1977; Thorpe, 1982; Ayala, 1986).

Over the past several years, we have been using the molecular genetic technique of microcomplement fixation (Champion et al., 1974) to assess molecular evolution in the Australian lizards. The study of the Varanidae with D. King and M. King is completed and will be published separately, while our work on the Gekkonidae and Pygopodidae has barely begun. However, our data on the Agamidae and Scincidae, although incomplete, are sufficiently extensive to provide a rough picture of their evolution in Australasia. We have taken the opportunity of the Bicentennial Herpetology Conference to present our preliminary data on these groups. Some aspects of the work we report here

on the Scincidae has involved S. Burgin, M. Hutchinson and C. Daugherty.

MATERIALS AND METHODS

Albumin was purified from plasma by disc electrophoresis and injected into rabbits (three per antigen) over a period of three months according to the schedule of Champion et al. (1974). Purity of antisera was checked by immunoelectrophoresis. The microcomplement fixation procedure followed the protocol of Champion et al., (1974). The results of cross-reactions are reported as Albumin Immunologic Distances (AIDs). One AID is roughly equivalent to one amino-acid substitution (Maxson and Wilson, 1974).

RESULTS

The Agamidae

Antisera were raised to six species of Australian agamids - *Ctenophorus vadnappa, Pogona barbata, Lophognathus gilberti, Moloch horridus, Gonocephalus bruynii* and *Physignathus lesueurii.* The full reciprocal matrix for these six taxa was corrected for reciprocity by the method of Cronin and Sarich (1975). The standard deviation for reciprocity (Maxson and Wilson, 1974) was 21.8% before correction and 8.2% after correction. The corrected reciprocal matrix is shown in Table 1. Also shown in Table 1 are the results of the one-way reactions to a range of other agamids from Australia, New Guinea, Asia, and Africa and two iguanids from North America.

The reciprocal data were used to produce an unrooted tree by the Fitch-Margoliash method (Fitch and Margoliash, 1967), using the PHYLIP 2.7 package written and kindly supplied by J. Felsenstein. To root this tree, an outgroup is needed. The outgroup must be close enough to be able to detect differential rates of evolution in the ingroup, but far enough away to be sure that it is an outgroup. The taxa tested for suitability as outgroups were *Agama aculeata, Calotes tympanostriga, Dipsosaurus dorsalis* and *Iguana iguana* (Table 1). Of these, only *Agama aculeata* was close enough to be useful as an outgroup.

Because we do not have immunological distances of all antisera to *A. aculeata*, it was not possible to produce a rooted tree for the Australian agamids using the Fitch-Margoliash criterion. However, we added *A. aculeata* to the tree by optimising the four distances available (Table 1). The resulting rooted tree for the Australasian agamids is shown in Fig. 1. This tree should be treated as provisional since it is based on incomplete data for *A. aculeata*, and has not been tested for robustness by jackknifing (Lanyon, 1985) . On the tree in Fig. 1, *Moloch* stands apart from the amphibolurids represented (*Pogona, Ctenophorus* and *Lophognathus*). However, the one-way reactions to other amphibolurids (*Chlamydosaurus* and *Diporiphora*) suggest that these genera fall outside a *Moloch/Pogona/Ctenophorus/Lophognathus* clade (Table 1). If this is true (and it needs to be tested by antisera to *Chlamydosaurus* and *Diporiphora*), then *Moloch* may in fact be part of the amphibolurid radiation. Moreover, again based on the one-way distance to *Chlamydosaurus* and *Diporiphora, Physignathus lesueurii* may be closely related to this clade.

A second feature of the one-way cross-reactions shown in Table 2 are the albumin distances to non-Australasian taxa. Of all the taxa tested, the African *Agama* is much closer to the Australasian agamids than are the Asian agamids, including, significantly, *Gonocephalus kuhli.*

The Scincidae

Antisera have been raised to 10 species of Australian skinks. A partial reciprocal matrix for these 10 species is shown in Table 2. Table 2 also shows the results of cross-reactions of these 10 antisera to a range of other skinks. Because the reciprocal matrix is as yet incomplete, it is not possible to correct for reciprocity by the method of Cronin and Sarich (1975), nor to construct phylogenetic trees by the Fitch-Margoliash method. Nevertheless, a number of perhaps unexpected features emerge from the limited data available. They are:

(1) The genus *Lampropholis* is highly diverse at the albumin level. AIDs among members of the genus range up to 29, which is as high as that characterising the entire amphibolurid radiation (see Table 2). Indeed, the species separated by 29 AIDs are *La. basiliscus* and *La. challengeri*, which are sibling species.

(2) The genus *Leiolopisma* is even more diverse at the molecular level, with AIDs up to 40! Indeed it is clear that the genus is not monophyletic. Some species of *Leiolopisma (entrecasteauxii, pretiosum, palfreymani* and *metallicum*) are closer to *Lampropholis* and *Carlia* than to other *Leiolopisma*, while *Le. duper-*

TABLE 1. Albumin immunologic distances (corrected for reciprocity) of antisera to six species of Australian agamids to a range of other agamids and iguanids. The standard deviation for reciprocity was 21.8% before correction and 8.2% after correction. CF is the correction factor.

	Antibody						Geographic origin
	Cv	Pb	Lg	Mh	Gb	Pl	
Antigen CF	0.70	0.79	0.98	1.64	1.03	0.89	
Ctenophorus vadnappa (Cv)	0	14	18	19	47	23	Australia
Pogona barbata (Pb)	10	0	18	21	42	21	Australia
Lophognathus gilberti (Lg)	24	14	0	23	39	26	Australia
Moloch horridus (Mh)	19	18	26	0	29	17	Australia
Gonocephalus bruynii (Gb)	43	42	40	27	0	33	New Guinea
Physignathus lesueurii (Pl)	26	25	23	19	29	0	Australia
Antigens only							
Tympanocryptis intima	17	14	20	23	48	35	Australia
Chlamydosaurus kingii	24	25	15	21	44	31	Australia
Diporiphora bilineata	31	33	30	26	50	33	Australia
Gonocephalus modestus	36	–	38	–	16	38	New Guinea
Gonocephalus kuhli	136	–	117	–	134	108	Asia
Calotes tympanostriga	169	–	157	–	139	–	Asia
Agama aculeata	71	–	68	56	71	–	Africa
Dipsosaurus dorsalis	163	–	–	–	141	–	North America
Iguana iguana	210	–	–	–	–	–	North America

reyi is closer to *Menetia* and *Morethia* than to other *Leiolopisma*. The New Zealand *Le. grande* forms a third group.

(3) The *Eugongylus* group of Greer (1979), here represented by *Eugongylus, Carlia, Lampropholis, Leiolopisma, Menetia, Morethia, Cryptoblepharus* and *Emoia*, appears to form a monophyletic group to the exclusion of *Egernia, Tiliqua, Sphenomorphus, Ctenotus, Mabuya, Lamprolepis, Tribolonotus* and, perhaps, *Mabuya*.

(4) Of the non-*Eugongylus* group species, *Egernia* and *Tiliqua* are close, but we have no data yet on possible relationships among other species.

DISCUSSION

The Agamidae

Current views of the biogeographical history of Australian and New Guinean agamids are highly disparate in some areas (cf. Tyler, 1979; Cogger and Heatwole, 1981; Witten, 1982). Briefly summarised, all schemes agree that there is an endemic component which is referred to as the amphibolurid radiation but whose composition varies between authors, and a group of genera (*Physignathus, Gonocephalus* and *Chelosonia*) which arose from Asian ancestors and have entered Australia recently from New Guinea.

The phylogenetic relationships of *Moloch* are not known with certainty, due to its highly autapomorphic morphology. *Moloch* has been considered as either the first agamid to have entered Australia and hence phylogenetically outside the amphibolurid radiation (Cogger and Heatwole, 1981), or as an embedded member of the endemic radiation (Witten, 1982). The albumin data support the latter, and moreover suggest that *Moloch* is well embedded in the amphibolurid radiation. Thus the hypothesis of a separate entry into Australia by *Moloch* is not supported by our data.

The origin of the supposedly Asian-derived species of *Gonocephalus* and *Physignathus* is also questioned by the albumin data. Most proposals in this area appear to have been strongly influenced by the current taxonomy. The albumin data suggest that the current taxonomy does not reflect the phylogenetic relationships of species in these genera. The New Guinean *Gonocephalus* available to us are *much* more closely related to the amphibolurids than to the Asian *Gonocephalus kuhli*. Similarly, *Physignathus lesueurii* is much more closely related to

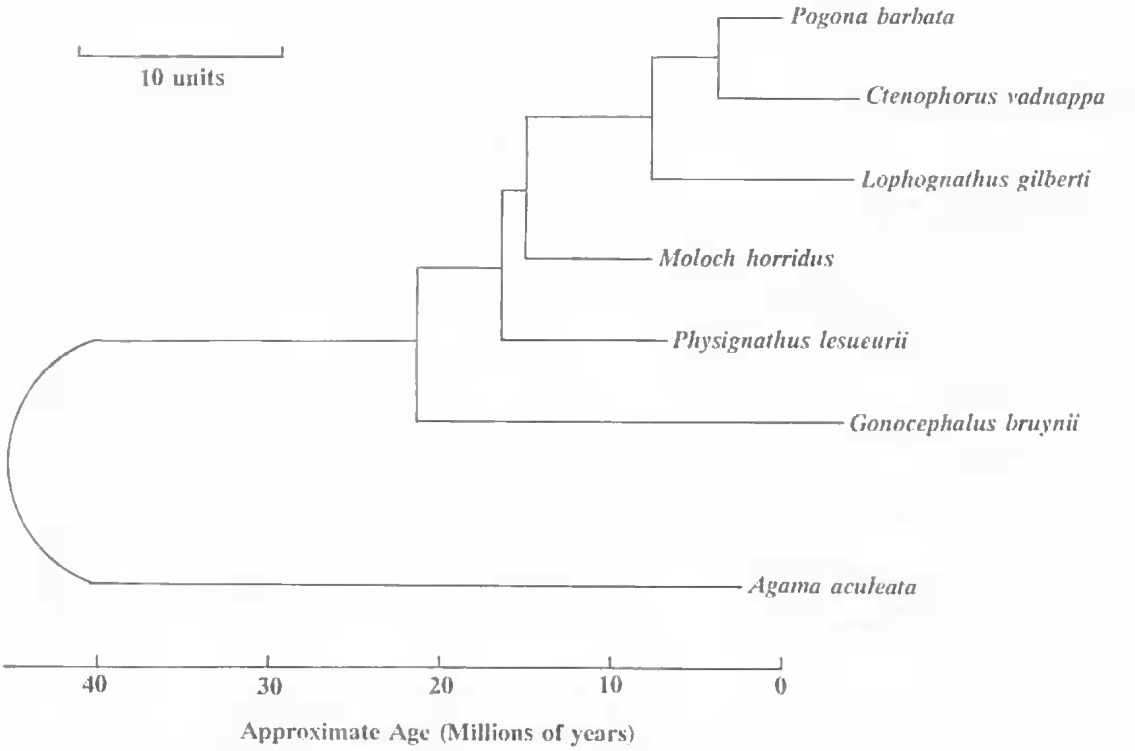


FIG.1. Phylogenetic tree, constructed by the Fitch-Margoliash method, among the six species of agamids to which antisera were raised. The tree was rooted using *Agama aculeata* as an outgroup. Branch lengths shown are proportional to the proposed amount of albumin change along each branch. An approximate time scale is given assuming T=0.6D.

the amphibolurids than to the available Asian genera. The only other member of the genus, *P. cocincinus*, is found in Indochina, and may not be very closely related to *P. lesueurii* (Witten, 1982). Hence the proposed recent Asian origin for these genera must be questioned critically in the light of the albumin data.

Taken at face value the tree in Fig.1 shows clear evidence that rates of albumin evolution within the Australasian agamids have been reasonably uniform among lineages. From the node common to all Australasian agamids, the range in amounts of albumin evolution vary from 12 units to *Moloch horridus* to 22 units to *Ctenophorus vadnappa*, a less than two-fold range. It is therefore appropriate to use a molecular clock for this data set. However, we need to calibrate the clock for agamids. Usually, such a calibration relies on obtaining from fossils an estimate of the age of at least one and preferably two cladogenic events in the history of the group. In order to date cladogenic events from fossil data, three requirements must be met. Firstly, the fossil must be well-dated, secondly, the fossil must be sufficiently well-preserved to be placed in a phylogenetic framework; thirdly, and most importantly, the systematics of extant forms must be well-established. Unfortunately, none of these requirements can be met for Australian agamids (Molnar, 1984).

The relationship T=0.6D (where T=time in millions of years and D=albumin immunologic distance) has been used frequently in the literature for a wide range of vertebrates including eutherians (Sarich, 1985), marsupials (Maxson et al., 1975), lizards and crocodiles (Gorman et al., 1971) and snakes (Cadle and Sarich, 1981), although usually without specifically calibrating the clock for the group in question. In the majority of cases, such a calibration has proved to be compatible with what limited available data there are for the group in question. Recently, however, Sarich (1985) has suggested that a relationship of T=0.37D is more appropriate for

TABLE 2. Albumin immunologic distances of antisera to 10 species of Australian skinks cross-reacted to a range of other skink species. The data are uncorrected.

	Antibody										Geographic
	Lac	Lag	Lab	Lad	Ma	Lep	Lea	Lee	Led	Ef	origin
Antigen											
Lampropholis challengeri (Lac)	0	17	29	23	45	14	17	30	40	—	Australia
Lampropholis guichenoti (Lag)	20	0	18	20	32	13	16	29	46	105	Australia
Lampropholis basiliscus (Lab)	17	13	0	12	—	—	—	—	—	—	Australia
Lampropholis cf. *delicata* (Lad)	21	19	25	0	—	—	—	—	—	—	Australia
Morethia adelaidensis (Ma)	59	62	49	46	0	36	46	28	29	—	Australia
Leiolopisma pretiosum (Lep)	—	—	—	—	30	0	6	18	37	—	Australia
Leiolopisma palfreymani (Lea)	20	16	23	12	—	5	0	17	35	—	Australia
Leiolopisma entrecasteauxii (Lee)	36	28	—	26	21	23	0	28	—	—	Australia
Leiolopisma duperreyi (Led)	67	51	49	47	22	35	40	26	0	—	Australia
Egernia frerei (Ef)	110	126	98	100	—	—	129	—	—	0	Australia
Antigens only											
Leiolopisma metallicum	17	16	24	21	—	4	9	—	—	—	Australia
Leiolopisma zia	24	22	29	14	—	14	13	25	47	—	Australia
Leiolopisma grande	45	41	44	35	—	29	—	—	34	—	New Zealand
Cryptoblepharus plagiocephalus	—	—	—	—	31	—	—	22	—	—	Australia
Carlia rostralis	28	21	26	24	—	27	22	38	39	—	Australia
Menetia greyi	60	50	48	46	21	38	41	35	10	—	Australia
Emoia longicauda	58	61	57	50	54	37	41	40	—	—	Australia/ New Guinea
Eugongylus rufescens	53	54	60	55	—	—	—	36	—	—	New Guinea
Sphenomorphus murrayi	94	104	85	—	—	—	—	—	—	—	Australia
Ctenotus grandis	110	117	94	96	—	—	103	—	—	—	Australia
Mabuya multifasciata	—	60	—	—	—	—	126	—	—	—	Indonesia
Lamprolepis smaragdina	114	120	90	—	—	—	—	—	—	—	New Guinea
Tribolonotus gracilis	—	120	140	—	—	—	—	—	—	—	New Guinea
Egernia kingii	—	—	—	—	—	—	—	—	—	17	Australia
Tiliqua rugosa	—	—	—	—	—	—	—	—	—	20	Australia

eutherian mammals, although Baverstock et al. (1989) have shown that such a relationship is not appropriate for marsupials. We herein use T=0.6D, although this relationship may need to be adjusted if and when relevant fossil data come to hand.

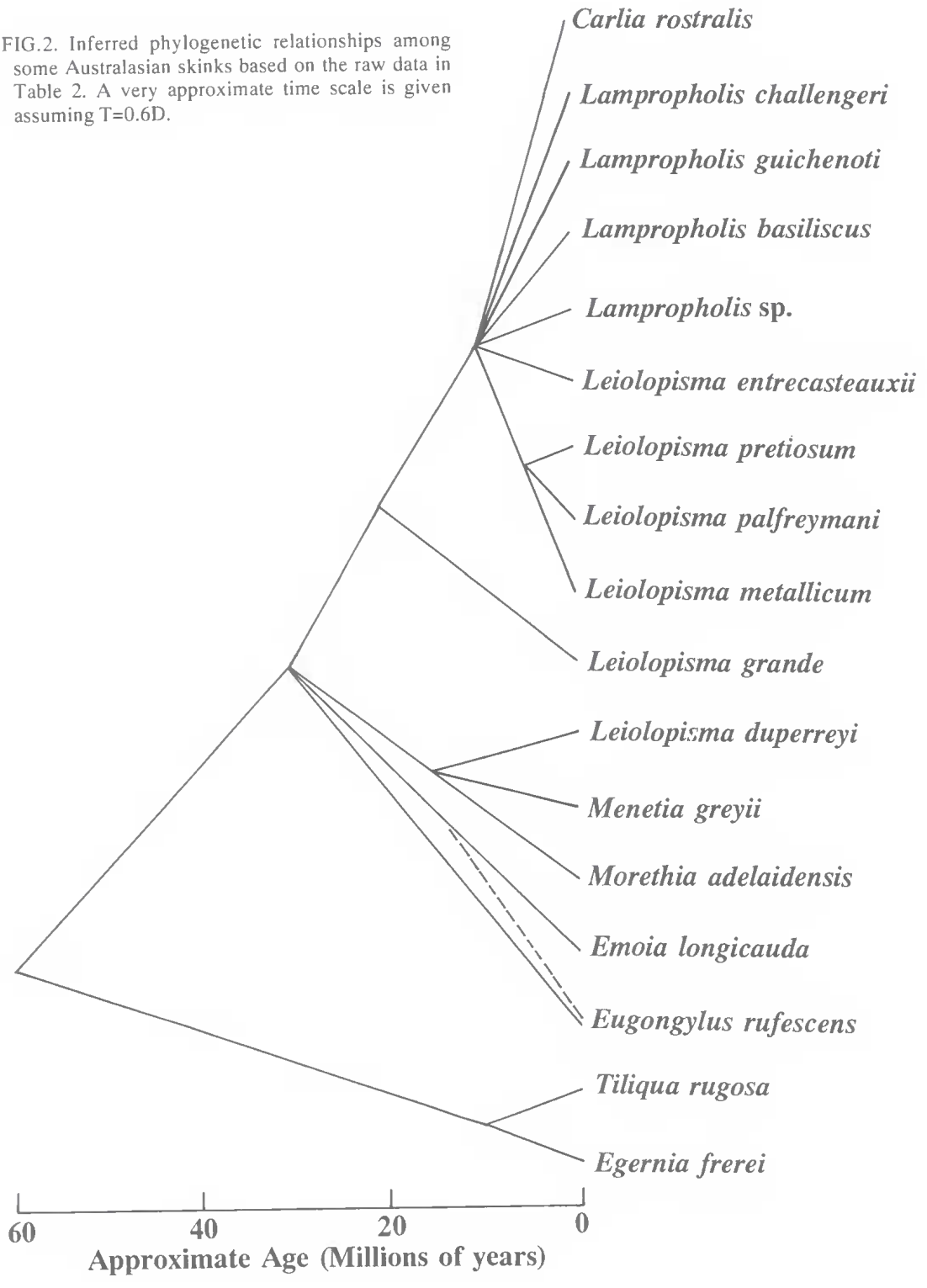
Fig. 1. shows an approximate time-scale for the Australasian agamid radiation, using T=0.6D. On this analysis, the three amphibolurids represented form a monophyletic group, radiating in the late Miocene-early Pliocene. However, the one-way data (Table 1) suggest that the radiation involving other amphibolurids (and *Moloch*) occurred a little earlier, perhaps mid-Miocene, and that the Australian *Physignathus* and *Gonocephalus* also diverged about this time.

Based on the phylogenetic relationships indicated by Fig.1 and Table 1, it is tempting to speculate that the Australasian agamids do indeed have a Gondwanan origin. On this scenario, the Australasian component gave rise to radiations in two land masses, Australia and what was to become New Guinea. The first gave the amphibolurid radiation (including *Moloch*) and the second to New Guinean *Gonocephalus* and *Physignathus*, which recently entered Australia. The morphological similarity of Asian and New Guinean *Gonocephalus* and *Physignathus* is then seen to be due to convergence. Using T=0.6D gives a divergence time of *Agama* from Australasian agamids of 40MY. This is much too short for a Gondwanan connection, but it is based on only one species of African agamid, one-way cross- reactions, and an untested calibration of T=0.6D. If the Australasian agamids do have an Asian origin, then the possible sister taxa are not Asian *Gonocephalus* and Asian *Physignathus*, and have not been included in our analyses.

The Scincidae

Most inferences of the biogeographic history of Australian skinks are based on the distribution of extant forms (the fossil record is virtually non-existent) and estimates of the time scale of cladistic events from comparisons of levels of faunal diversity (Greer, 1979; Tyler, 1979; Cogger and Heatwole, 1981). It has been amply

FIG.2. Inferred phylogenetic relationships among some Australasian skinks based on the raw data in Table 2. A very approximate time scale is given assuming T=0.6D.



demonstrated that speciation and morphological clocks do not exist (Baverstock and Adams, 1987) and hence estimates of time based on these are purely speculative. Additionally, if the current systematics does not accurately reflect the phylogenetic relationships then inferences based on the distribution of such groups can be erroneous. Greer (1979), Tyler (1979) and Cogger and Heatwole (1981) concur that skinks arose north of Australia's present day position and Greer (1979) and Cogger and Heatwole (1981) propose that the ancestors of the scincid radiation entered Australia at least twice. Cogger and Heatwole (1981) suggest that the earliest invaders were here by at least the mid-Tertiary. The finding of fossil cranial elements from the mid-Miocene referable to the extant genus *Egernia* (Estes, 1984) at least gives a minimum age of entry which is compatible with this view.

The microcomplement fixation data suggest some anomalies in the current systematics and provide a rough estimate of the timing of evolutionary events. However, our data are as yet not extensive enough at the suprageneric level to provide information relevant to the evolutionary origins of the skink fauna of Australia. Fig.2 is summary cladogram of the relationships among some Australian skinks that seem to be indicated by the data in Table 2. We do stress however that these proposed relationships are very tentative, and will undoubtedly be refined as additional antigens and antisera are added to the data set. We have also added a very approximate time scale assuming T=0.6D is an appropriate calibration for the Australian skinks.

While our data provide strong support for a monophyletic *Eugongylus* group, they are at odds with Greer's (1979) concept of two subgroups within the *Eugongylus* group. If indeed there are two subgroups present then their compositions are vastly different from those conceived by Greer (1979). Several authors concur that the genus *Leiolopisma* is composite (Rawlinson, 1974; Greer, 1982). Our data demonstrate that this is so, but the groups delineated do not agree with previous schemes. *L. duperreyi* is more closely related to *Morethia* and *Menetia* than to other *Leiolopisma*. Greer (1980) had previously suggested such a relationship but later included *L. duperreyi* in his *L. baudini* species group which included *L. entrecasteauxii* and *L. metallicum*, species not especially related by the microcomplement fixation data.

Hutchinson (1980) from immunoelectrophoretic comparisons and a reappraisal of Greer's (1979) morphological assessment suggested that the spiney skinks of the genus *Tribolonotus* are probably closest to the *Eugongylus* group. While our data on *Tribolonotus* are based at this stage on one-way comparisons, they do not provide strong support for such a view, and instead suggest that *Tribolonotus* is at least as divergent from the *Eugongylus* group as *Egernia* and *Lamprolepis*.

While the present study shows that the genus *Leiolopisma* is at least paraphyletic, nevertheless the New Zealand representative of the genus available to us (*Le. grande*) is clearly a member of the *Eugongylus* group, with a divergence time from its nearest Australian relatives of about 20 MYBP. Thus a Gondwanan origin for New Zealand *Leiolopisma* is clearly rejected by the albumin data, which support Hardy's (1977) view of a more recent invasion of New Zealand from Australia.

CONCLUDING REMARKS

We have been struck by the highly disparate pattern of morphological and molecular genetic evolution in the Australian skinks and agamids. In the skinks, morphologically similar species are nevertheless highly divergent at the molecular level. This feature is emphasised in the genus *Lampropholis*, where sibling species have albumins that differ by up to 20 amino-acids. By contrast, the agamids show morphological diversity in the face of relative uniformity at the albumin level. Species as diverse at the morphological level as bearded dragons (*Pogona*), thorny devil (*Moloch*), and frilled-neck lizard (*Chlamydosaurus*) are nevertheless as similar at the molecular level as sibling species of *Lampropholis*.

These contrasts highlight the vast disparity between morphological evolution and molecular evolution, a feature which has been noted in other groups (e.g. Maxson and Wilson, 1974; Wilson et al., 1977; Baverstock and Adams, 1987). While rates of molecular evolution may vary a little between different groups (perhaps two- or threefold: see Brownell, 1983; Wu and Li, 1985), it is apparent that rates of morphological evolution can vary enormously between groups. Thus estimates of divergence times and biogeographic reconstructions that rely upon considerations of morphological diversity alone are unlikely to be valid.

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